3   Structured populations

In all dynamical models considered so far, we have assumed that all individuals behave equally with respect to the population dynamics. All have the same birth and death rates, and all contribute to competition in the same way. Although for the discrete dynamics, we did consider individuals at different life stages (juveniles and adults), this only had an indirect effect on the recurrence equation $F(N)$. Indeed, there was at least one time point during the life cycle when all individuals were equivalent (adults just before giving birth). We could thus use this life stage for the dynamics, while other stages (juveniles) were "integrated out". However, this is no longer possible if individuals at different life stages coexist at all times.

Age structure and Leslie matrices   The typical example is a population with an age-structured demography. Let x_i the number (or density) of individuals in age-class i, $i \in \{1, \dots, n\}$. Let p_i be the survival probability from age class i to $i+1$ and let f_i be the fertility (expected number of offspring) of each member of age-class i. Then

$$x_{i+1}(t+1) = p_i x_i(t) \quad i = 1, \dots, n-1 \tag{1}$$

$$x_1(t+1) = \sum_i f_i x_i(t) \tag{2}$$

which can be summarized as

$$\mathbf{x}(t+1) = \mathbf{L}\mathbf{x}(t) \tag{3}$$

with the Leslie matrix (Leslie 1945)

$$\mathbf{L} = \begin{pmatrix} f_1 & f_2 & \cdots & f_{n-1} & f_n \\ p_1 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & \cdots & 0 & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & 0 & \cdots & p_{n-1} & 0 \end{pmatrix} \tag{4}$$

Other examples of structure

1. Spatial structure: A population lives in a structured habitat. Birth and death rates depend on the local characteristics and there is migration among the demes.

2. Different genotypes: Birth and death rates depend on the heritable genotype. Transition between genotype classes can occur due to mutation during reproduction.

3. Size structure: instead of age as such, for many species (like trees) the size is the more decisive factor.

- In general, the art of modeling is to decide which structure best describes a population. It is not necessary that individuals in one class have all the same demographic parameters: we can consider average quantities. However: these average quantities should only depend on the state the individuals are in and *not* on the history (i.e., where they came from): We thus want to make sure that the population dynamics can be described by a generalized *Markov model* (but note that the transition matrix is not normalized).

- We can illustrate all these models as graphs. Arrows between states represent non-zero transition probabilities. The transition matrix is also called the population projection matrix.

General formalism: linear model Let $x_i(t)$ the number of individuals in class i at time t, $i \in \{1, \ldots, n\}$. Let $m_{ij} := m_{i \leftarrow j}$ be the transition rate from state j to state i and $\mathbf{M}$ the corresponding population projection matrix. We assume that the transition rate (= demographic parameters) are constant. We thus consider a (time)-homogeneous process. In particular, we also assume ignore any density- or frequency-dependence. We then have a linear model with explicit solution

$$\mathbf{x}(t) = \mathbf{M}^t \mathbf{x}(0).$$ (5)

We ask the following questions:

- What is the long-term growth rate of the population? Do we get growth or extinction?

- What kind of distribution over the states x_i does result in the long run? $\longrightarrow$ Analog to stationary distribution of a Markov process.

Definitions: Irreducible, primitive, spectral radius

- A non-negative matrix $\mathbf{M}$ is called *irreducible* if for each pair $[i, j]$ there is some $k(i, j) \in \mathbf{N}$, such that $[\mathbf{M}^{k(i,j)}]_{i,j}$ is positive.

Biologically, a population projection matrix is irreducible if and only if a path exists from every state to any other state in the corresponding (life-cycle) graph. Most population models are irreducible. Exceptions are life-cycles with post-reproductive states and spatially structured models with sources and sinks.

- A non-negative matrix $\mathbf{M}$ is called *primitive* if there is some $k \in \mathbf{N}$, such that $\mathbf{M}^k$ is positive.

Obviously, primitive implies irreducible. Irreducible, but non-primitive projection matrices are characterized by loops in their corresponding graphs. An irreducible matrix $\mathbf{M}$ is primitive if and only if the greatest common divisor of the loop lengths is 1. Sufficient conditions for an irreducible matrix to be primitive are (1) any self-loop (2) positive fertility of adjacent age-classes in a Leslie matrix.

- The spectral radius of a matrix $\mathbf{M}$ is $r(\mathbf{M}) := \max_i |\lambda_i|$, where $\lambda_1, \ldots, \lambda_n$ are the eigenvalues of $\mathbf{M}$.

Theorem: Perron-Frobenius (Perron 1907, Frobenius 1912) Let $\mathbf{M} := (m_{ij})_{1 \leq i,j \leq n}$ a matrix with real, non-negative entries $m_{ij} \geq 0$. Then

1. $\mathbf{M}$ has a real leading eigenvalue $\lambda_1 = r(\mathbf{M})$ (called dominant EV). Right and left eigenvectors $\mathbf{v}$ and $\mathbf{u}$ corresponding to λ_1 with non-negative entries exist.

2. If further $\mathbf{M}$ is *irreducible*, it has a dominant EV $\lambda_1 > 0$, which is simple (has geometric and algebraic dimension one). All entries of the corresponding eigenvectors $\mathbf{v}$ and $\mathbf{u}$ are strictly positive.

3. Assume further that $\mathbf{M}$ is *primitive*. Then λ_1 is *strictly dominant*, i.e., larger than all other eigenvalues, $\lambda_1 > |\lambda_i|$, $i \neq 1$.

Proof

(a) **Convergent matrices**
For any (square) matrix $\mathbf{M}$,

$$r(\mathbf{M}) < 1 \quad \Leftrightarrow \quad \mathbf{M}^k \to \mathbf{0} \quad \text{for } k \to \infty \tag{6}$$

Proof: Obvious for any matrix $\mathbf{D}$ in Jordan from and $\mathbf{M}^k = \mathbf{S}\mathbf{D}^k\mathbf{S}^{-1}$ (a matrix $\mathbf{M}$ with this property is called *convergent*).

(b) **Lower bound for the spectral radius**
Let $\mathbf{M} \geq 0$ and $\mathbf{0} \neq \mathbf{v} \geq 0$ and $\lambda \geq 0$. Then

$$\forall i : \ [\mathbf{M}\mathbf{v}]_i = \sum_{j=1}^{n} m_{ij} v_j > \lambda v_i \ \Rightarrow \ r(\mathbf{M}) > \lambda. \tag{7}$$

Proof: $\exists \epsilon > 0 : \ \mathbf{M}\mathbf{v} > (\lambda + \epsilon)\mathbf{v}$ (for every component). Thus

$$\mathbf{v} < \frac{\mathbf{M}}{\lambda + \epsilon}\mathbf{v} < \left(\frac{\mathbf{M}}{\lambda + \epsilon}\right)^2 \mathbf{v} < \left(\frac{\mathbf{M}}{\lambda + \epsilon}\right)^k \mathbf{v} \quad \forall k > 2$$

because $\mathbf{M}\mathbf{v}$ with $m_{ij} \geq 0$ is monotonic in every component v_i. For $k \to \infty$ we see that $\mathbf{M}/(\lambda + \epsilon)$ has a lower bound and is thus not convergent. With (a) we conclude that $r(\mathbf{M}) \geq \lambda + \epsilon > \lambda$.

(c) **Positivity of the leading eigenvalue and -vector**
Let $\mathbf{M} > 0$ and λ_1 eigenvalue with $|\lambda_1| = r(\mathbf{M})$. Then $\lambda_1 = r(\mathbf{M})$ and any corresponding right eigenvector is strictly positive, $\mathbf{v} > 0$ (up to a common scalar factor for all entries of $\mathbf{v}$). The same holds for any dominant left eigenvector.
Proof: Let $\lambda_1 \mathbf{v} = \mathbf{M}\mathbf{v}$ and assume that the entries of $\mathbf{v}$ are not collinear in the complex plane (where collinear means positive real or zero up to a common scalar factor). Then

$$|\lambda_1||v_i| = \left| \sum_{j=1}^{n} m_{ij} v_j \right| < \sum_{j=1}^{n} m_{ij}|v_j| \quad \forall i = 1, \ldots, n.$$

Thus $|\lambda_1||\mathbf{v}| < \mathbf{M}|\mathbf{v}|$ (in each row) and thus $|\lambda_1| < r(\mathbf{M})$ due to (b), contradicting the assumption. Thus all entries of $\mathbf{v}$ are collinear and can be chosen as ≥ 0. Since

$$\sum_{j=1}^{n} m_{ij} v_j = \lambda_1 v_i$$

also λ_1 must be real and positive. Since $m_{ij} > 0$, we also have $v_i > 0 \, \forall i$. Proof for the left eigenvector follows by switching to $\mathbf{M}^T$.

(d) **Geometric and algebraic dimension of the dominant eigenvalue**
Let $\mathbf{M} > 0$. Then the geometric and algebraic dimension of the dominant eigenvalue $\lambda_1 = r(\mathbf{M})$ is one.
Proof: Geometric: Assume that there are two eigenvectors $\mathbf{v}$ and $\mathbf{w}$ corresponding to λ_1. Then a linear combination $\mathbf{v} + \kappa \mathbf{w}$ exists with at least one component zero, contradicting (c). The proof for the left eigenvector follows again by switching to $\mathbf{M}^T$. Algebraic: Assume that $\mathbf{w}$ exists, such that $(\mathbf{M} - \lambda_1 \mathbf{I})^2 \mathbf{w} = 0$, but $(\mathbf{M} - \lambda_1 \mathbf{I})\mathbf{w} \neq 0$ (generalized eigenvector). Then $\mathbf{x} = (\mathbf{M} - \lambda_1 \mathbf{I})\mathbf{w}$ is an eigenvector of $\mathbf{M}$ with eigenvalue $\lambda_1 = r(\mathbf{M})$. Due to (c) we can choose $\mathbf{x} > 0$. Let $\mathbf{u} > 0$ be the dominant left eigenvector. Then we obtain a contradiction with

$$0 = \mathbf{u}^T \cdot (\mathbf{M} - \lambda_1 \mathbf{I})\mathbf{w} = \langle \mathbf{u}; \mathbf{x} \rangle > 0 \,.$$

Remark: This proves the Perron-Frobenius Theorem for strictly positive matrices.

(e) **Primitive matrices**
Let $\mathbf{M}$ be primitive and $\mathbf{M}^k > 0$. Let λ_1 be some eigenvalue of $\mathbf{M}$ with $|\lambda_1| = r(\mathbf{M})$ and corresponding eigenvector $\mathbf{v}$. Then $\mathbf{v}$ is also eigenvector of $\mathbf{M}^k$ with eigenvalue $\lambda_1^k = r(\mathbf{M}^k)$. From the theorem for positive matrices we know $\mathbf{v} > 0$, thus also λ_1 is strictly dominant, real and positive and has dimension one. This proves part 3 of the Theorem.

(f) **Irreducible matrices**
Let $\mathbf{M}$ be irreducible. Then $\mathbf{M} + \epsilon \mathbf{I}$ is primitive. Let $\lambda_\epsilon = \lambda + \epsilon$ be the strictly dominant eigenvalue of $\mathbf{M} + \epsilon \mathbf{I}$ with corresponding eigenvector $\mathbf{v}$. Note that $\mathbf{v}$ does not depend on ϵ and is, in particular, also eigenvector of $\mathbf{M}$ with eigenvalue λ. Since $\mathbf{v} > 0$, we must have $\lambda > 0$. Since $\epsilon \mathbf{I}$ just shifts the spectrum, λ has dimension one and we have $\lambda = r(\mathbf{M})$ due to continuity, but other eigenvalues $|\tilde{\lambda}| = r(\mathbf{M})$ may exist.

(g) **Non-negative matrices**
Let $\mathbf{M} \geq 0$ and $\epsilon > 0$. The theorem for positive matrices holds for any matrix $\mathbf{M}_\epsilon = (m_{ij} + \epsilon)_{1 \leq i,j \leq n}$. Let $\lambda_\epsilon = r(\mathbf{M}_\epsilon)$ be the strictly dominant eigenvalue and $\mathbf{v}_\epsilon > 0$ the corresponding eigenvector. For $\epsilon \to 0$ we get $\mathbf{v}_\epsilon \to \mathbf{v} \geq 0$, where $\mathbf{v}$ is eigenvector of $\mathbf{M}$ with eigenvalue $\lambda = r(\mathbf{M})$. Note that λ need not be strictly dominant and its dimension need not be one.

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3.1 Long term behavior

Consider the linear population dynamics

$$\mathbf{x}(t) = \mathbf{M}^t \mathbf{x}(0) \,. \tag{8}$$

Assume first that $\mathbf{M}$ is primitive. (This is the case for most models.) Then there is a strictly dominant eigenvalue $\lambda_1 = r(\mathbf{M})$ with positive left and right eigenvectors $\mathbf{u}_1$ and $\mathbf{v}_1$. We can normalize these according to $\|\mathbf{v}_1\| = 1$ and $\langle \mathbf{u}_1; \mathbf{v}_1 \rangle = 1$. We then have

$$\left(\frac{\mathbf{M}}{\lambda_1}\right)^t \longrightarrow \mathbf{v}_1 \otimes \mathbf{u}_1^T \quad \text{for } t \to \infty \,. \tag{9}$$

If $\mathbf{M}$ can be diagonalized with eigenvalues $\{\lambda_i\}_i$, and corresponding sets of left and right eigenvectors, $\{\mathbf{u_i}\}_i$ and $\{\mathbf{v_i}\}_i$, respectively, with $\langle \mathbf{u}_i; \mathbf{v}_j \rangle = \delta_{ij}$. Then

$$\mathbf{M}^t = \sum_{i=1}^{n} \lambda_i^t \, \mathbf{v}_i \otimes \mathbf{u}_i^T \,. \tag{10}$$

Proof. Let $\mathbf{U}$ be the orthogonal complement of the vector $\mathbf{u}_1^T$. Note that $\mathbf{M}$ maps $\mathbf{U}$ onto itself. Let $\mathbf{M}'$ be the restriction of $\mathbf{M}$ to $\mathbf{U}$. Then the spectral radius of $\mathbf{M}'/\lambda_1$ is smaller than one, and the matrix hence convergent. Since $\mathbf{v}_1$ is not orthogonal to $\mathbf{u}_1$ we can chose $\mathbf{v_1}$ and any basis of $\mathbf{U}$ as basis of the full vector space. The proof follows from the action of $(\mathbf{M}/\lambda_1)^t$ on this basis in the limit $t \to \infty$. The proof of (10) is analog, using the pairwise orthogonality of sets of left and right eigenvectors. It also holds if $\mathbf{M}$ is not primitive.

Consequences.

- For any population vector $\mathbf{x}(0)$ and any irreducible matrix $\mathbf{M}$ observe that $\langle \mathbf{u}_1; \mathbf{x}(0) \rangle > 0$. For any primitive matrix $\mathbf{M}$ we then obtain the long-term growth rate

$$r_\infty = \lim_{t \to \infty} \frac{\|\mathbf{x}(t+1)\|_1}{\|\mathbf{x}(t)\|_1} = \lambda_1 \lim_{t \to \infty} \frac{\|(\mathbf{M}/\lambda_1)^{(t+1)}\mathbf{x}(0)\|_1}{\|(\mathbf{M}/\lambda_1)^t\mathbf{x}(0)\|_1} = \lambda_1 \,. \tag{11}$$

- The limit distribution reads

$$\lim_{t \to \infty} \frac{\mathbf{x}(t)}{\|\mathbf{x}(t)\|_1} = \mathbf{v}_1 \,. \tag{12}$$

  For age structured models, this is also called a stable age structure.

- We can estimate the rate at which the limit distribution is approached by considering the second largest eigenvalue $|\lambda_2|$, as follows

$$r_t = r_\infty + C\big(\mathbf{x}(0)\big) \left|\frac{\lambda_2}{\lambda_1}\right|^t \tag{13}$$

  with a constant C that depends on the initial conditions. An analog results holds for the limit distribution.

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- For any irreducible, but periodic matrix, Eq. (11) still holds, but there is no unique limit distribution (12). We can still characterize the long-term behavior by considering all eigenvectors to eigenvalues $|\lambda_i| = r(\mathbf{M})$ and their linear combinations.

- For reducible matrices, we first try to identify absorbing states or subspaces and then consider the dynamics on irreducible subsystems defined by this absorbing states and their complements.

3.2 Eigenvalues of Leslie matrices

In general, it is difficult (or impossible) to derive the eigenvalues and eigenvectors of high-dimensional matrices. For the special form of the Leslie matrix, however, this is simplified. Here, we have from $\mathbf{Lx} = \lambda \mathbf{x}$,

$$p_1 x_1 = \lambda x_2 \quad \Rightarrow \quad x_2 = \frac{p_1}{\lambda} x_1 \tag{14}$$

$$p_2 x_2 = \lambda x_3 \quad \Rightarrow \quad x_3 = \frac{p_2}{\lambda} x_2 = \frac{p_1 p_2}{\lambda^2} x_1 \tag{15}$$

$$p_{n-1} x_{n-1} = \lambda x_n \quad \Rightarrow \quad x_n = \frac{p_{n-1}}{\lambda} x_{n-1} = \frac{p_1 \cdots p_{n-1}}{\lambda^{n-1}} x_1 \tag{16}$$

We thus have

$$\lambda x_1 = f_1 x_1 + \ldots + f_n x_n \tag{17}$$

$$= x_1 \left(f_1 + f_2 \frac{p_1}{\lambda} + f_3 \frac{p_1 p_2}{\lambda^2} + \ldots + f_n \frac{p_{n-1} \cdots p_1}{\lambda^{n-1}} \right). \tag{18}$$

If we define the probability for a newborn to survive until age i as $l_1 = 1$ and $l_i = p_1 \cdots p_{i-1}, i > 1$, we obtain the so-called Euler-Lotka equation

$$1 = \sum_{i=1}^{n} f_i l_i \lambda^{-i} =: \phi(\lambda). \tag{19}$$

The Euler-Lotka equation relates the asymptotic growth rate (also called the fitness of an individual) to the life-history parameters f_i and p_i (or l_i). It is easy to see that the expression on the right-hand-side is strictly monotonically decreasing. We thus obtain exactly one solution for a real eigenvalue $\lambda = r(\mathbf{L})$. One can further show that Leslie matrices are always diagonalizable; all other eigenvalues are complex. There is still no general explicit solution for λ_1, but we can at least determine whether $\lambda_1 > 1$ (the population is growing) or $\lambda_1 < 1$ (shrinking) population. For this, define the life-time reproductive success $R_0 = \sum_i f_i l_i$. We see that R_0 is the value of the Euler-Lotka equation at $\lambda = 1$. From the shape of the graph, we immediately see that $\lambda_1 > 1 \Leftrightarrow R_0 > 1$ (which makes intuitive sense). Once we know λ, it is easy to obtain the corresponding eigenvector

$$\mathbf{v}_1 = \left(\frac{l_1}{\lambda_1}, \frac{l_2}{\lambda_1^2}, \ldots, \frac{l_n}{\lambda_1^n} \right)^T \tag{20}$$

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3.3 Application: Life history evolution

Typical problems of life history theory are as follows:

- Why do we age? Why are there widely different life spans among species?

- At a given age class: is it better to invest into survival or into reproduction?

- Is it better to have many offspring once or fewer offspring more often during life?

All these problems ask why certain life-history parameters in a Leslie matrix take their given values. We can try and approach this problem from an evolutionary point of view: Consider a resident population that is characterized by a certain set of life-history parameters. Assume now that a mutant appears in this population with a different set of parameters. We can always ask: Will the mutant replace the resident? To answer this question, we first need to know how individuals of different types compete and how population regulation is included into our framework of structured models. Since this leads to non-linear models, this can be very complicated, indeed! So simplify things, we will assume here that population regulation occurs in an independent step and affects all individuals in the same way, i.e.,

$$\mathbf{x}(t) \ \rightarrow \ \mathbf{x}(t + 1/2) = \mathbf{L}\mathbf{x} \ \rightarrow \mathbf{x}(t + 1) = f(N)\mathbf{x}(t + 1/2) \tag{21}$$

where $N = \sum_i x_i$ is the total population size and $f(N)$ takes care of density regulation. For example we could have

$$f(N) = \frac{1}{1 + cN} . \tag{22}$$

This scheme has two important properties

1. First, since density regulation acts only as a factor on the population vector, it does not alter the distribution. In the long term, we will thus reach the same stable age distribution as with the linear model.

2. Assume now that this stable age distribution has been reached. We then have

$$N(t + 1) = \lambda N(t) \cdot f(N(t)) \tag{23}$$

   where λ is the long-term growth rate of the linear model.

We thus can separate our problem and treat both parts (age distribution and density regulation) independently. Indeed, this is also the reason why models without age structure make some sense at all. We simply assume (implicitly) that a stable age distribution has been reached. Now, what will happen with a rare mutant in such a case? (We assume no recurrent mutation)

- A mutant will start its own clone and both clones will reach a stable age distribution. Since they are subject to joint density regulation, the clone with the higher limiting growth rate (higher fitness) will win and displace the other type.

Example: Iteroparous versus semelparous reproduction   Why do many plants and some animals reproduce only once in their lifetime and then die (semelparous reproduction), while others reproduce multiple times (iteroparous reproduction)? – In principle, being able to reproduce multiple times is of course be an advantage and should be selected. However, there may be a cost: concentration on a single reproduction event could increase the expected litter size. In a much simplified version, compare two strategies:

1. On the one hand, consider an immortal iteroparous clone with fertility f_{it} every season.

2. On the other hand, consider a semelparous clone, where individuals reproduce after the first season with fertility f_{sem} and then die.

How large must f_{sem} be that the semelparous clone matches the growth rate of the iteroparous clone? (Assume that all our results can be extended to infinite dimensional matrices in this case.)

- Iteroparous: Euler-Lotka equation

$$1 = f_{it} \sum_{i=1}^{\infty} \lambda^{-i} = f_{it} \frac{\lambda^{-1}}{1 - \lambda^{-1}}$$

and hence $\lambda = f_{it} + 1$

- Semelparous:

$$1 = f_{sem} \lambda^{-1}$$

and thus $\lambda = f_{sem}$.

We thus see that only a single individual more in the first year is worth as much as eternal life and offspring every year. The question arises why there are so many iteroparous species! More generally, we can derive the predictions for an adult survival probability p_a and a juvenile survival probability p_j. Here, we assume that p_j is the probability that juveniles survive even until the first census. then p_j acts like a factor to the fertility. We obtain:

- Iteroparous:

$$1 = f_{it} p_j \sum_{i=1}^{\infty} (p_a^{(i-1)} \lambda^{-i})$$

and thus $\lambda = p_a + p_j f_{it}$.

- Semelparous:

$$1 = f_{sem} p_j \lambda^{-1}$$

thus $\lambda = f_{sem} p_j$.

We get equal long-term growth rates for

$$f_{\text{sem}} = f_{\text{it}} + \frac{p_a}{p_j} \,.$$

This leads to the prediction that species with a higher ratio of adult / juvenile survival probability should more likely be iteroparous (or have more breeding seasons, on average). This is, indeed, confirmed by data.

3.4 Reproductive values and sensitivity analysis

How important are the different (age-)classes for the population growth? Or: How much does an individual in the initial population contribute to future population growth? We have

$$\mathbf{x}(t) \approx \lambda^t \mathbf{v} \sum_i u_i x_i(0) \tag{24}$$

where $\mathbf{v}$ is the leading right eigenvector and u_i are the entries of the leading left eigenvector. We thus see that the u_i are weighting factors that determine the importance of age-class i for future population growth. They are called *reproductive values*. For the Leslie matrix, we can derive the reproductive values as follows. Let u_1 be the reproductive value of newborns. In the distant future, the clones started from any individual at time zero will grow with factor λ per time step. But initially, the relative growth rates are different. We can relate the size of a clone started from an individual in age class i to the size of a clone started from a newborn as follows:

$$u_i = \left(\frac{f_i}{\lambda} + \frac{l_{i+1}}{l_i} \frac{f_{i+1}}{\lambda^2} + \frac{l_{i+2}}{l_i} \frac{f_{i+2}}{\lambda^3} + \ldots + \frac{l_n}{l_i} \frac{f_n}{\lambda^{n-i+1}} \right) u_1 \tag{25}$$

$$= \frac{\lambda^{i-1}}{l_i} \sum_{j=i}^n l_j f_j \lambda^{-j} u_1 \,. \tag{26}$$

The factors λ^j in the denominator accounts for the delay of j time steps for the newborn offspring individuals produced by our focal individual in age class i. Note that the equation for u_1, in particular, reproduces the Euler-Lotka equation. With the choice $u_0 = \lambda$, we have

$$u_i = \frac{\lambda^i}{l_i} \sum_{j=1}^n l_j f_j \lambda^{-j} \tag{27}$$

Typically, the reproductive value increases until an individual reaches maturity and then decreases. For post-fertility age-classes it is zero. Reproductive values also tell us how severe perturbations in the number of individuals in a given age class are for future population dynamics (relevant for population management). Another use of the reproductive value is in sensitivity analysis.

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Sensitivity analysis In general, we can ask, which demographic parameter "matters most" for the long-term growth rate. In an evolutionary perspective, this corresponds to the parameters that experience the strongest selection pressure. For a general projection matrix $\mathbf{M} = (m_{ij})_{1 \leq i,j \leq n}$, the answer is given by the so-called sensitivities

$$s_{ij} := \frac{\partial \lambda}{\partial m_{ij}} . \tag{28}$$

Frequently, sensitivities are measured on a scale of relative change rather then absolute change. We then obtain the so-called elasticities

$$e_{ij} := \frac{\partial \log \lambda}{\partial \log m_{ij}} = \frac{m_{ij}}{\lambda} s_{ij} . \tag{29}$$

With

$$\lambda = \frac{\mathbf{u}^T \cdot \mathbf{M} \mathbf{v}}{\mathbf{u}^T \cdot \mathbf{v}} \tag{30}$$

we simply get

$$s_{ij} = \frac{u_i v_j}{\mathbf{u}^T \cdot \mathbf{v}} . \tag{31}$$

In general, if several entries of the projection matrix depend on some model parameter x, $m_{i,j} = m_{i,j}(x)$, we obtain the sensitivity with respect to any such x as a linear combination of the s_{ij},

$$s_x = \frac{\partial \lambda}{\partial x} = \sum_{i,j} s_{ij} \cdot \frac{\partial m_{i,j}}{\partial x} . \tag{32}$$

For Leslie matrices $\mathbf{M} = \mathbf{L}$, we have

$$\mathbf{u}^T \cdot \mathbf{v} = \sum_{k=1}^{n} \sum_{j=k}^{n} l_j f_j \lambda^{-j} = \sum_{k=1}^{n} k \, f_k l_k \lambda^{-k} \tag{33}$$

and hence

$$s_{ij} = \frac{(l_j/l_i) \lambda^{i-j} \sum_{k=i} l_k f_k \lambda^{-k}}{\sum_{k=1}^{n} k \, l_k f_k \lambda^{-k}} . \tag{34}$$

In particular, this gives

$$\frac{\partial \lambda}{\partial f_j} = s_{1j} = \frac{l_j \lambda^{1-j}}{\sum_{k=1}^{n} k \, l_k f_k \lambda^{-k}} \tag{35}$$

and

$$\frac{\partial \lambda}{\partial p_j} = s_{j+1,j} = \frac{(l_j/l_{j+1}) \lambda \sum_{k=j+1}^{n} l_k f_k \lambda^{-k}}{\sum_{k=1}^{n} k \, l_k f_k \lambda^{-k}} . \tag{36}$$

We can make the following observations

- Early-in-life fecundities are under stronger selection than late-in-life fecundities (for $\lambda \geq 1$).

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- Also selection on viabilities monotonically decreasing and only > 0 as long as the fertility later in life is still positive. As a consequence, we have weak sekection against deleterious mutations with an effect late in life: evolutionary explanation for senescence and death.

- Assume that there is a trade-off between viability and fecundity at age i. We have

$$\left(\frac{\partial \lambda}{\partial p_j}\right) / \left(\frac{\partial \lambda}{\partial f_j}\right) = u_j / \lambda \tag{37}$$

Thus, age classes with high reproductive value should invest more into survival than age classes with low reproductive value. In particular, survival at maturity is more strongly selected than survival of newborns.

3.5 Other formalisms to model population structure

We have discussed in some detail the projection matrix approach to population structure. This formalism works in discrete time and it assumes that the ppopulation can be structured into discrete classes. Both of these assumptions are convenient, but analogous approaches, which do not make these assumptions also exist. This leads either to so-called *Lotka integral equation* or to the *McKendrick-von Foerster partial differential equation*. Similar to the matrix approach, both formalisms allow for (partial) solutions as long as the dynamics is linear. In general, also similar conclusions can be drawn.